ZOOLOGIA 34: e20785
ISSN 1984-4689 (online)
zoologia.pensoft.net

RESEARCH ARTICLE

Population ecology of *Chaetophractus vellerosus*: the first report for an armadillo in South America

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http://zoobank.org/8AC22CEA-D394-48BD-B141-B381AF9CA871

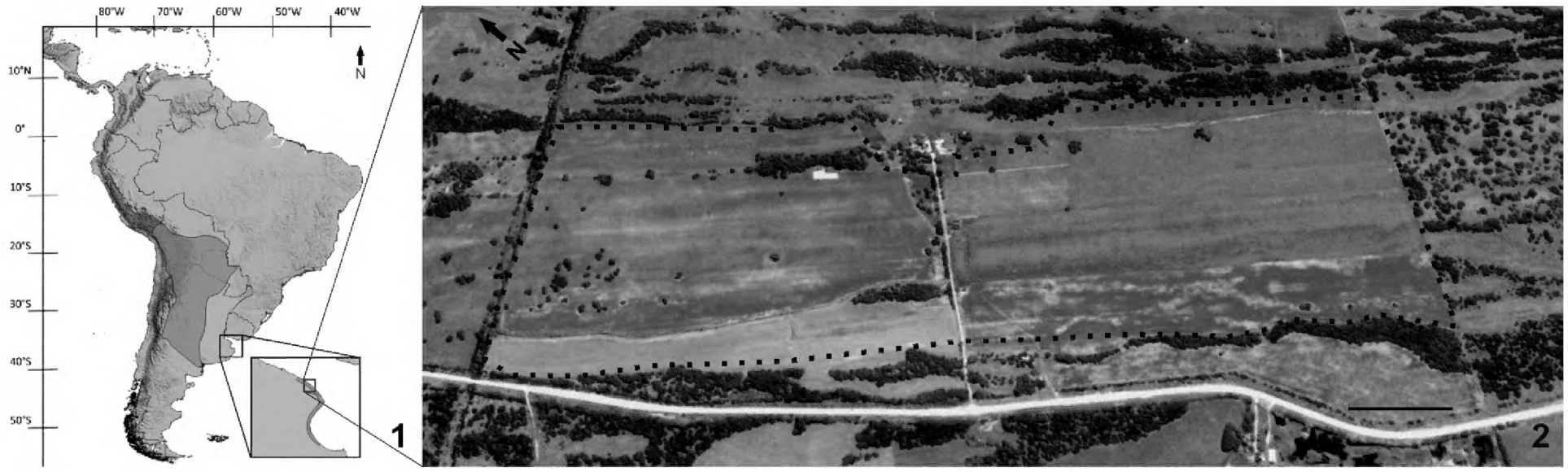
ABSTRACT. The aim of this work was to obtain the first estimates of survival rates (*S*), capture probability (*p*) and life expectancy for armadillos in South America by analyzing capture-mark-recapture data obtained from a population of *Chaetophractus vellerosus* (Gray, 1865) located in Magdalena, Buenos Aires, Argentina. From June 2006 to June 2011, we conducted 16 field surveys that resulted in 365 capture events of 152 adult *C. vellerosus*. For the survival analysis we used a Cormack-Jolly-Seber (CJS) modelling framework. Interannual variation in *S* made an important contribution to overall variation in the survival rate of *C. vellerosus*. The average life expectancy for females and males after attaining sexual maturity was estimated at 1.70 and 1.65 years respectively. The period of lowest survival probability was associated with dry seasons that might have affected the availability of food. This study provides the first estimates of demographic parameters for xenarthrans in South America.

KEY WORDS. Argentina, capture probability, CMR, screaming hairy armadillo, survival rates.

INTRODUCTION

Armadillos are one of the most distinctive mammals of South America, and the only group that originated in this continent. Although these singular animals have attracted the attention of travelers and naturalists since the 15th century, the development of scientific studies on their ecology and other topics is very scarce (Superina et al. 2014, Loughry et al. 2015). Despite many years of field work involving armadillos, there are currently only two reports that provide estimates of demographic parameters (Loughry et al. 2013a, b). Both involved the study of the same, single population of a single species, *Dasypus novemcinctus* Linnaeus, 1758, that was located outside of its native range. This undoubtedly stems, at least in part, from the fact that armadillos are cryptic, asocial, primarily nocturnal, burrowing, and cannot be captured with commercial traps (see Loughry and McDonough 2013, Loughry et al. 2013a, Superina et al. 2014).

Chaetophractus vellerosus (Gray, 1865) is an armadillo that has an considerable amount of data available on its diet, home range, thermoregulation, activity pattern, distribution, genetics, and physiology (Abba et al. 2007, 2015 and references therein, Abba and Cassini 2010, Abba and Vizcaíno 2011, Pagnutti et al. 2014, Nardelli et al. 2016). *Chaetophractus vellerosus* has a disjunct population found in the northeast of the Pampa region, which is separated from the main distribution area by about 500 km (Crespo 1974, Carlini and Vizcaíno 1987, Abba et al. 2011) (Figs 1, 2). This relict population is associated with the shelly beach ridges on the coast of the Río de la Plata River, covering an area of less than 900 km^2 (Abba and Superina 2010), where it faces a high risk of extinction due to habitat modification and use by humans (Abba et al. 2007, 2014). Therefore, estimates of the population parameters for this isolated group would be extremely useful for conservation purposes.



Figures 1–2. (1) Geographical range of *Chaetophractus vellerosus* and location of the relict population in Magdalena, Buenos Aires Province. Map was extracted from IUCN SSC Anteater, Sloth and Armadillo Specialist Group, *C. vellerosus*. The IUCN Red List of Threatened Species. (2) Satellite image of the fields where the armadillos were captured. The dotted line represents the boundaries of the study area. Scale bar: 250 m.

The aim of this work was to obtain the first estimates of survival rates for armadillos in South America by analyzing capture-mark-recapture (CMR) data obtained between 2006 and 2011 for adult individuals from a portion of the isolated population of *C. vellerosus* that was located in Magdalena, Buenos Aires province (Argentina), and to establish the effect of sex and interannual variation on adult survival rates.

MATERIAL AND METHODS

We sought to capture armadillos within a 100 ha area located in an agricultural field (Figs 1, 2). This field was selected based on a previous study that documented considerable signs of armadillo activity there (Abba et al. 2007). Our capture and marking techniques followed those developed by Loughry and McDonough (2013) for *D. novemcinctus*. From June 2006 to June 2011, we conducted 16 field surveys. In the first years, surveys were conducted from 9:00 am to 7:00 pm, with two surveys in each of the four seasons of the year, with the exception of winter of 2007 when only one survey was conducted (a total of nine surveys in 2006–2007). In 2008 only one survey was conducted (during the summer) due to logistic constraints. From 2009 onward we made two surveys per year, one that involved sampling at night during the summer (7:00 pm to 1:00 am, three surveys total), and the other sampling during the day in winter (10:00 am to 6:00 pm, three surveys total). This change in methodology was based on data collected during the first two years of our study (2006, 2007), in which we detected a switch in the behavior of the animals between hot and cold seasons, but found that the intermediate seasons (fall and spring) did not show different patterns (Abba et al. 2011).

For each survey, three field observers walked 30-m-wide transects until the entire sampling area was covered; total sampling effort for all surveys was 61 days (4–5 days per survey) and 1500 hours of field time. During surveys, we attempted to capture and process (i.e., measured and marked) all armadillos that were detected during a survey. All burrows with signs of recent activity (e.g., accumulation of grass, soil that had been removed, etc.) were sampled to check for the presence of armadillos; this check consisted of a visual inspection of the initial 50 cm of the burrow. Animals were captured by hand or in a net and burrows were checked by hand or, on occasion, by opening the first 50 cm with a shovel. During the first two years of the study the ears of the animals were marked with numbered ear tags (National Band and Tag Company, Newport, KY, #1005-1); subsequently animals were marked using a passive transponder system (Trovan ID-100). For temporary identification we used a sticker affixed to the carapace, which allowed us to follow the animals after release and avoid recapturing them again on the same day. Age was estimated using body length and weight (Abba et al. 2011).

We used a Cormack-Jolly-Seber (CJS) modelling framework (Lebreton et al. 1992) to estimate survival rates (S) and capture probability (p) of adult individuals. Although juvenile and adult survival rates are expected to be different (e.g. Loughry et al. 2013a), available field data on juvenile did not allow us to fit a CJS model including an estimate of pre-adult survival rate. Therefore, we decided it was best to model adult survival rate alone instead of polling pre-adult and adult data, because if it were the case that juvenile and adult survival do differ, the resulting estimates of survival rate will not be representative of adults or juveniles.

The CJS model was chosen because its assumptions best fit some important features of our study system. CJS models do not take into account migration, i.e., they assume a geographically closed population (Lebreton et al. 1992). In the presence of migration, the survival rates estimated by CJS models actually vary not only with mortality rate but also with emigration rate,

and thus are usually referred to as apparent survival. This was not an issue in our study because the field site is bounded on the west by the Provincial Route #11, to the east by the Rio de la Plata Estuary and to the north and south by two artificial canals that flow into this Estuary. These boundaries represent physical barriers to dispersal for screaming hairy armadillos, therefore making it a virtually isolated population (see Figs 1, 2 and Nardelli et al. 2016). Consequently, we assumed migration rates to be negligible in the population, and that estimates of survival parameters corresponded to actual survival rates. Due to logistic constraints, our field surveys varied both in capture effort and in the time between consecutive samples. Accordingly, we included the time period between consecutive field surveys as input to the models; varying capture effort was taken into account by constructing candidate models, as described next.

The set of candidate models was constructed as follows. We included the sex of individuals and the year in which a survey was conducted as potential effects to account for variation in survival rate. Capture effort was not constant among field surveys, as previously noted. Thus, to account for variation in capture probability, in addition to the sex of individuals as a potential effect, we included an indicator of the campaign for each field survey. Candidate models were constructed that included independent effects on survival rates and capture probability, and that considered both first-order effects and interactions between all effects. In order to explore the effect of interannual variation on survival rates, we considered time periods of one year that started and ended in winter (i.e., June of one year to July of the following year). However, this was problematic for the two-year period between June 2007 to June 2009. We therefore decided to retain the 2008 data, but to make only one estimate of survival probability for the entire 2007–2009 period. We felt this was reasonable because the low number of captures in the 2008 field survey, where only seven adult individuals were caught, provided insufficient data to make reliable estimates of survival probability for a one-year period.

CJS models are based on the binomial distribution, and as such do not independently model mean and variance. When fitting a capture-recapture model, it is not uncommon that observed variance is greater than expected, a phenomenon known as overdispersion (Anderson et al. 1994). Overdispersion can be taken into account by including an extra parameter known as the overdispersion coefficient ($\hat{c}$) in the models, which has a value >1 if overdispersion actually occurs. We tested for overdispersion by comparing the deviance of the most general candidate model with results obtained by fitting the same model to simulated data with known values of overdispersion (White et al. 2001). The test yielded an estimate of $\hat{c} < 1.1$, indicating overdispersion did not occur.

Model selection was performed using an information-theoretic approach following Burnham and Anderson (2002). The Akaike Information Criteria ranks candidate models based on a balance between how well a model fits the data but also on its complexity (i.e., the number of free parameters), because a more complex model will tend to fit the data better just by chance alone. The Akaike Information Criteria with correction for small sample size (AICc) was computed for each candidate model. These values were subsequently used to compute Akaike weights, which can be interpreted as the probability of the model being correct considering the whole set of candidate models (Burnham and Anderson 2002). Next, multi-model inference by model-averaging was performed by computing the weighted average of S and p across all fitted models using the Akaike weights as weighting factors, obtaining mean and 95% confidence intervals (CI). To allow comparison between multi-model survival probability estimates in a standard way, a Tukey's test (Sokal and Rohlf 1995) was performed using means and standard errors in the logit scale used in the CJS model fitting procedure, although it is worth noting that such classical test of significance lies outside the information-theoretic approach (Burnham and Anderson 2002). In addition, we performed an estimate of the average survivorship curve for *C. vellerosus* for adult individuals of both sexes using the results of the CJS models as follows. We used the parameter estimates from the model with the lowest Akaike information criterion that included sex as the only effect on survival probability, thus neglecting temporal variation. By definition, this model provides the best estimates of the survival probability for adult individuals, subject to the constraint that survival is constant over time, thereby providing an estimate of average survival over the entire span of the field work. Using the estimated survivorship curve, average life expectancy and median life expectancy were computed following Fox (2001): numerical integration using a daily time step was used to determine the proportion of individuals expected to die by a certain age, with average life expectancy computed as the mean of age at death, and median life expectancy as the age by which 50% of individuals are expected to have died.

The CJS models were fitted using program MARK (White and Burnham 1999), which was also used to compute the overdispersion test, AICc and Akaike weights. Multi-model inference computations were made in Microsoft Excel using the output from MARK software. Computation of survivorship curves were performed using the free software GNU Octave 3.8.2 (Eaton et al. 2009).

RESULTS

A total of 152 adult individuals were caught, 82 females and 70 males, in a total of 365 capture events (Table 1). The CJS models that best explained capture-recapture data according to the Akaike information criteria are presented in Table 2. The models that accounted for >79% of the cumulative Akaike weight included an effect of interannual variation on survival probability, indicating that this factor made an important

Table 1. Descriptive summary of annual field surveys for *Chaetophractus vellerosus* in Magdalena, Buenos Aires Province, Argentina.

	2006–2007	2007–2009	2009–2010	2010–2011
Adults individuals captured	74	76	29	34
Sex	43♀–31♂	40♀–36♂	16♀–13♂	17♀–17♂
Capture events	117	131	43	74
Sampling effort (days)	16	21	10	14

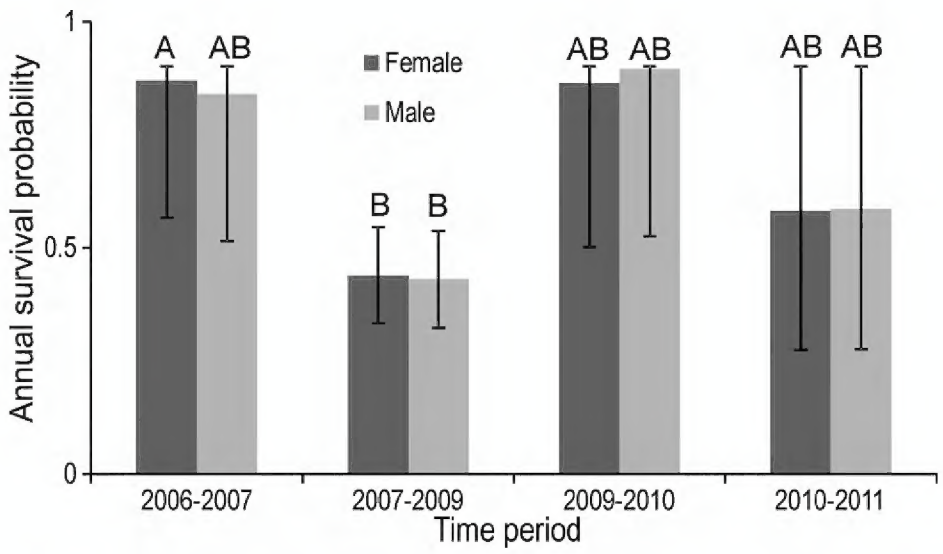


Figure 3. Temporal variation in annual survival probability of *Chaetophractus vellerosus*, estimated by multi-model inference based on the set of candidate CJS models. Error bars correspond to 95% confidence intervals, and letters (A and B) denote statistically homogeneous subsets ($P > 0.05$).

contribution to overall variation in the survival rate of adult *C. vellerosus* individuals. In contrast, the effect of sex on survival probability was included in models that accounted for only 28% of the cumulative Akaike weight. Regarding capture probability, the top CJS models that accounted for >99% of the cumulative Akaike weight included the effect of campaign, as expected due to the variable sampling effort in each field survey, whereas the effect of sex was of much lesser impact, and was included in models that collectively account for only 24% of the cumulative Akaike weight.

In order to examine the effect of interannual variation on survival probability, a multi-model inference scheme was followed. The estimated annual survival probabilities were similar between sexes, but strongly varied between study periods (Fig. 3). Highest annual survival was estimated for the 2006–2007 and 2009–2010 periods, with means in the 0.84–0.90 range, whereas lowest values obtained for 2007–2009 had a mean 0.43. However, due to a large variation in annual survival estimates, significant differences were only found for the 2006–2007 value for females compared to 2007–2009 for both sexes. Estimates of weekly capture probability were similar between sexes but strongly varied between field survey campaigns, and ranged from extreme values of 0.028 (0.004–0.19 95% C.I.) on the last campaign in 2006–2007 to 0.84 (0.27–0.94 95% C.I.) in the first campaign of 2010–2011 (Fig. 4). Since the duration of field surveys varied between years (Table 1), to explore a potential bias we made a graphical inspection and found no obvious as-

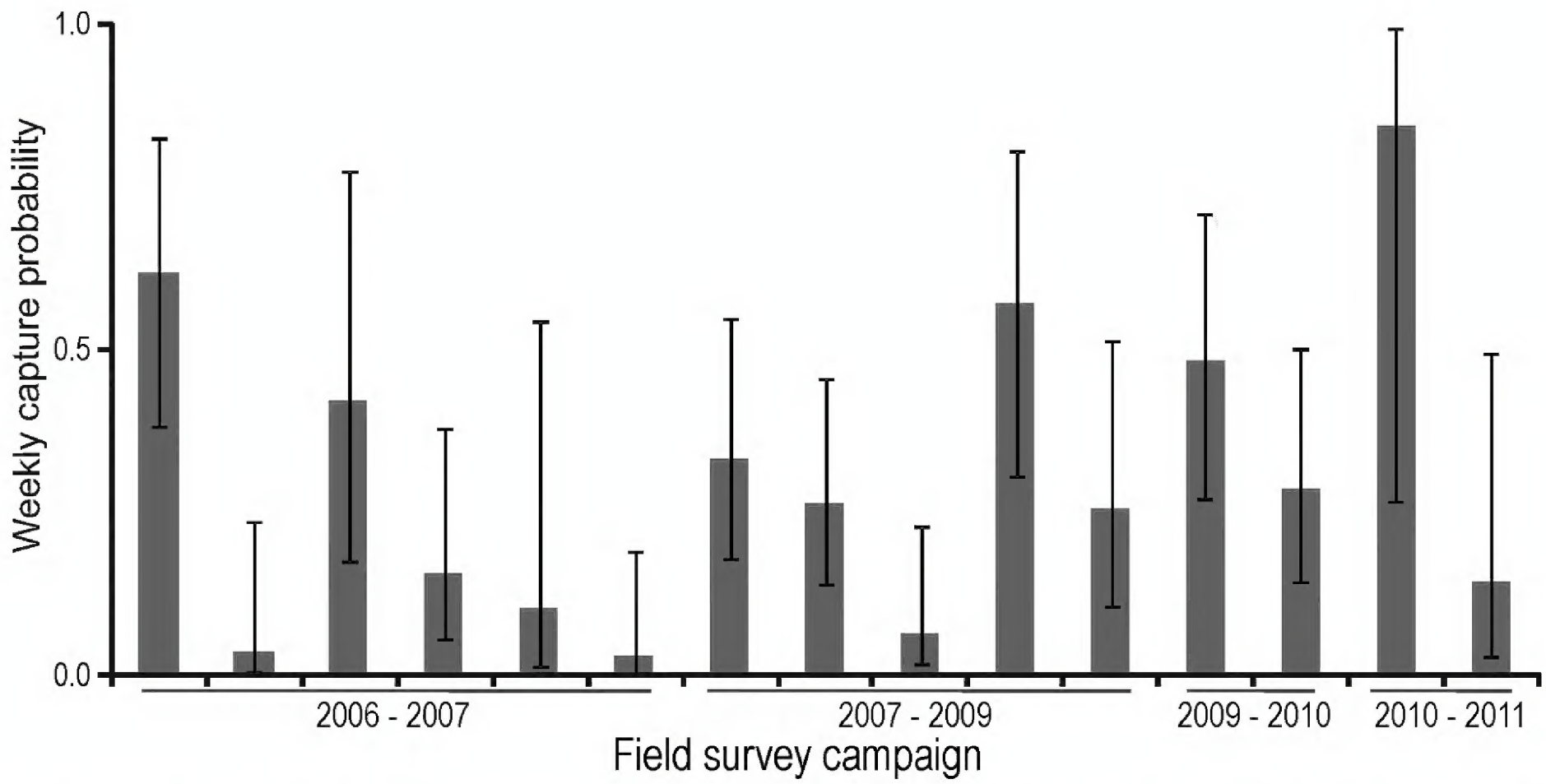


Figure 4. Mean values (± SE) of weekly capture probability (*p*) for adult *Chaetophractus vellerosus* for each field survey, estimated by multi-model inference based on the set of candidate CJS models. Values are presented for both sexes combined because differences in capture probability between males and females were in all cases < 3%.

Table 2. CJS models fitted to the capture-recapture data of *Chaetophractus vellerosus*, ranked according to the Akaike information criterion. Note that only the top 9 out of 25 candidate models are presented, which collectively accounted for >0.99 of the cumulative Akaike weight. Model structure is indicated by listing between parentheses which variables affect survival rates (*S*) and capture probability (*p*), using a single point (.) when no variable has an effect.

	Model	Parameters	Deviance	AICc	ΔAICc	Model likelihood	AICc Weight
1	*S* (year) *p* (campaign)	19	289.6	636.2	–	1.00	0.40
2	*S* (.) *p* (campaign)	16	298.7	638.4	2.18	0.34	0.13
3	*S* (year) *p* (sex + campaign)	20	289.4	638.5	2.21	0.33	0.13
4	*S* (sex + year) *p* (campaign)	20	289.5	638.6	2.32	0.31	0.12
5	*S* (sex x year) *p* (campaign)	23	284.2	640.4	4.16	0.12	0.05
6	*S* (sex + year) *p* (sex + campaign)	21	289.2	640.6	4.35	0.11	0.05
7	*S* (.) *p* (sex + campaign)	17	298.7	640.7	4.44	0.11	0.04
8	*S* (sex) *p* (campaign)	17	298.7	640.7	4.46	0.11	0.04
9	*S* (sex x year) *p* (sex + campaign)	24	283.8	642.5	6.21	0.04	0.02

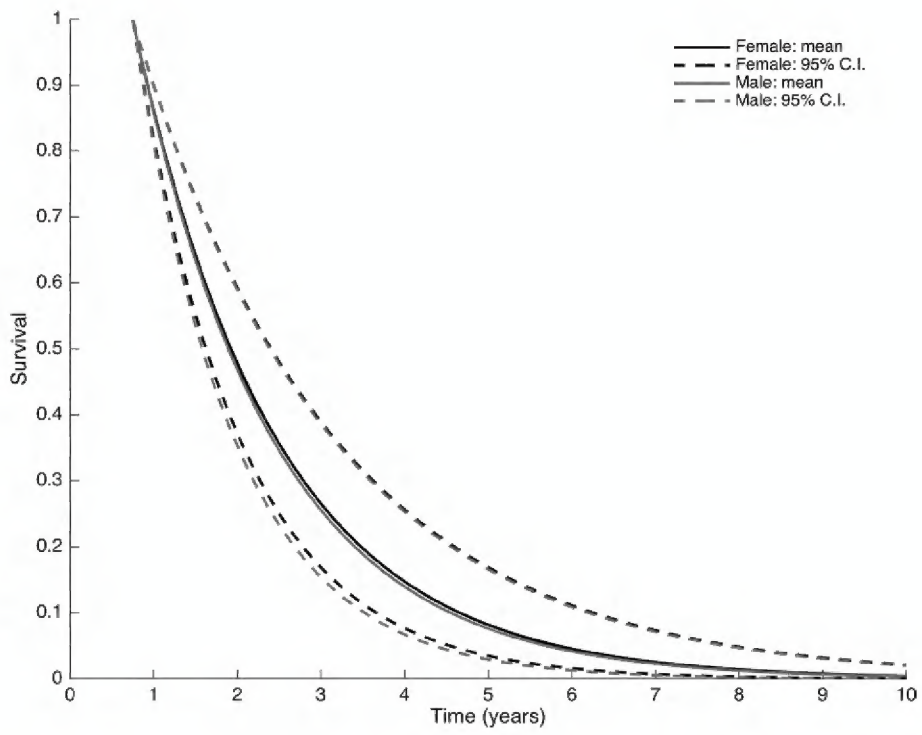


Figure 5. Projection of a survivorship curve for *Chaetophractus vellerosus* adult individuals of both sexes, assuming constant survival, from an age of nine months old, when sex maturity is achieved (Nowak 1991), to 10 years old. Solid lines correspond to mean and dotted lines correspond to 95% confidence intervals (black = female, grey = male).

sociation between survival probability estimates and sampling effort, although the reduced number of cases prevented the use of a formal statistical test.

The projected survivorship curves for *C. vellerosus* adult individuals over the entire study period showed a similar pattern for both sexes (Fig. 5). Based on the projected survivorship curves, the average life expectancy after attaining sexual maturity for females and males was estimated at 1.70 (1.27–2.38 95% C.I.) and 1.65 (1.20–2.36 95% C.I.) years respectively, while the projected median life expectancy once sexual maturity is attained was 1.18 (0.88–1.66 95% C.I.) and 1.14 (0.84–1.64 95% C.I.) years.

DISCUSSION

This study provides the first estimates of demographic parameters for xenarthrans in South America, and just the second study of the population ecology of armadillos overall (and, importantly, the first for *C. vellerosus*). Survivorship curves for males and females were presented and are only the second to have been calculated for any species of armadillo.

As previously pointed out, the only study dealing with the population ecology of xenarthrans was performed by Loughry et al. (2013a) in *D. novemcinctus*, and estimated an annual survival probability for adults between 0.701 (± 0.020, non reproductive females) to 0.753 (± 0.034, males and reproductive females). They observed that this parameter was partially influenced by sex and the life stage, with juveniles and yearlings exhibiting lower annual apparent survival than adults. We only included adults in our study so we cannot assess age effects on survival. However, we did show that adult survival was influenced by year, which could be the result of varying environmental conditions. The period of lowest survival probability was 2007–2009, which was associated with a dry season of < 700 mm of precipitation. This was substantially lower than the historical mean of 1000 mm of annual precipitation (SMN, Exp_144540). These dry conditions might have affected the availability of food, leading to the negative effect on survival probability. Aside from this dry period, we obtained values of survival probability that were quite similar to those reported for *D. novemcinctus* adults (Loughry et al. 2013a), which may suggest that such values represent a general feature that applies to many species of armadillos.

On the other hand, the capture probability (*p*) of *D. novemcinctus* (Loughry et al. 2013a) was best described with an additive effect of stage (age class), sex, and time, indicating stage- and sex-specific differences, as well as temporal variation. In our study *p* was influenced by the campaign, thus demonstrating a strong, and not surprising, effect of sampling effort. Put simply, as expected, with more days of field work, more armadillos are caught.

In the present study the influence of sex on survival probability was not significant compared with temporal variability. This is consistent with a range of studies conducted previously that have found few differences between male and female *C. vellerosus* in traits such as morphology, diet, home range, etc. (Abba et al. 2011, Pagnutti et al. 2014).

The survivorship estimate for *C. vellerosus* presented here can be compared with that provided by Loughry et al. (2013b) for *D. novemcinctus*. Those authors obtained a life expectancy estimate of 3 years for juvenile and yearling individuals, almost twice our estimate. Because *D. novemcinctus* is three to four times bigger than *C. vellerosus* (4.2 vs. 0.8 kg, Loughry and McDonough 1996, Abba et al. 2011), the difference in estimations of life expectancy could be due to a size scaling phenomena (Glazier 2005). In concordance with the data obtained by Loughry et al. (2013b), we do not believe we have severely underestimated life expectancy. Of a total of 74 adults captured in the 2006–2007 period, four individuals (5.4%) were recaptured during 2010–2011, which is roughly in accordance with an estimated 6.8% based on the average survivorship for a 4.5 years duration (3.4–12.8 95% C.I.). If our estimate is legitimate, then it will be an interesting challenge for future work to determine the details of how survival and future reproduction influence the population dynamics of armadillos.

The results of this work suggest that the survival rate is similar for adult individuals of both sexes, and that temporal variability is the main driver of variation in the survival of *C. vellerosus*. Therefore, it will be important for future studies to both confirm these trends, and to unravel the influences of environmental variables such as precipitation, temperature and atmospheric pressure that seem to be important factors in *C. vellerosus* biology (Abba et al. 2011). Because in this study only adult survival rate was estimated due to low number of captures of juveniles, future field work should be conducted from October to December in order to obtain more information about juveniles. Finally, the genetic data presented by Nardelli et al. (2016), that found in the same population of the present work three groups of individuals that are genetically differentiated, raise the question of whether the genetically differentiated subgroups found within our isolated, relict population exhibit similar population parameters and dynamics.

ACKNOWLEDGEMENTS

We thank L.G. Pagano and M.C. Ezquiaga for their assistance during fieldwork, and Lic. Ana Teresa Gómez (Jefe Departamento, CIM, SMN) for her support with the climatic data (SMN, Exp_144540). We appreciate the improvements in English usage made by W. J. Loughry and the valuable comments. We also want to thank two anonymous reviewers for valuable input that helped us to improve the manuscript. This work was partially supported by the Agencia Nacional de Promoción Científica y Tecnológica (BID PICT2010-1412) and Universidad Nacional de La Plata (PPID/N004).

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Submitted: 23 November 2016
Received in revised form: 4 April 2017
Accepted: 9 May 2017
Editorial responsibility: Diego Astúa de Moraes

Author Contributions: AMA designed the survey and conducted field work; VVB and SRD analyzed the data; AMA, VVB and SRD wrote the paper.

Competing Interests: The authors have declared that no competing interests exist.